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WOOD ANATOMY OF CNEORACEAE:
ECOLOGY, RELATIONSHIPS, AND GENERIC DEFINITION

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ABSTRACT

Wood anatomy of the three species of *Cneorum* is described qualitatively and quantitatively. The species differ in features related to ecology and form a clear series in this regard. The wood features of the family can all be matched by some Rutaceae and Simarubaceae, and the characteristics of Cneoraceae are listed in this connection. Nearly as many features are shared by Cneoraceae with Anacardiaceae and Sapindaceae; certain distinctive features may be found in somewhat more distant families, such as Oxalidaceae. Resemblances between Cneoraceae and Euphorbiaceae are attributed at least in part to the fact that Euphorbiaceae comprise a highly heterogeneous family with respect to wood anatomy. Wood anatomy of the three species of *Cneorum* diverges markedly. These differences when tabulated show that the Cuban species *C. trimerum* is the most distinctive. *Cneorum pulverulentum* (Canary Islands) and *C. tricocon* (northwestern Mediterranean coasts), although distinct in wood anatomy, resemble each other more closely than they resemble *C. trimerum*. Despite the distinctive tetramerous flowers and hexacolpate pollen of *C. pulverulentum*, a single genus seems advisable; *C. trimerum* cannot be readily segregated on the basis of gross morphology.

Key words: Cneoraceae, *Cneorum*, ecological wood anatomy, Rutales, Sapindales, wood anatomy.

INTRODUCTION

Cneoraceae have been treated as a monogeneric family containing three species: *Cneorum pulverulentum* Vent. (lowlands of five of the Canary Islands: Bramwell and Bramwell 1974); *C. tricocon* L. (Mediterranean coasts of Spain, France, Balearic Islands, Sardinia, and northern Italy: Tutin, Heywood, Burges, Moore, Valentine, Walters, and Webb 1968); and *C. trimerum* (Urb.) Chodat (Sierra Maestra, Oriente, Cuba: Sauget and Liogier 1951). These habitats range from rather moist tropical to dry Mediterranean; thus, comparisons between wood anatomy and ecology are appropriate.

Heimsch (1942) studied wood anatomy of Cneoraceae in his investigation of the woods of the orders Gruinales and Terebinthales. Heimsch's work is accurate, but it is supplemented here with quantitative and certain qualitative details. Only twig material was available to Heimsch for two of the species, and mature stems of these are used in the present study. Heimsch's conclusion that wood of Cneoraceae resembles that of Rutaceae more closely than that of Zygophyllaceae is valid. A more detailed series of comparisons is attempted here in an effort to place Cneoraceae as precisely as possible.

The three species of *Cneorum* prove to have notably divergent patterns of wood anatomy. This has led me to reassess the generic constitution of the family. The distinctive tetramerous flowers of *C. pulverulentum* led Tieghem (1899) to segregate that species as *Chamaelea*. Erdtman (1953) discovered that the species differs from *C. tricocon* by having hexacolpate rather than tricolpate pollen, and

affirmed this genus, which he renamed *Neochamaelea* for nomenclatural reasons. The evidence from wood anatomy complicates this picture, and the generic treatment of the family is therefore reassessed here.

MATERIALS AND METHODS

Two collections of *C. pulverulentum* were made in the wild in 1968 on the island of Tenerife: *Carlquist 2482* (Barranca del Infierno) and *Carlquist 2530* (Teno). These were supplemented by a collection kindly provided by Dr. David Bramwell from the Jardín Botánico Canario "Viera y Clavijo," Tafira Alta, Gran Canaria. This latter collection has the merit of representing a specimen from cultivation, and therefore showing if features alter as a result of cultivation. The results obtained below show no differences. This validates the use of a specimen of *C. tricocon* from cultivation: the specimen *Carlquist 20-VI-1971* was cultivated in Orpet Park, Santa Barbara, California. However, the area of the Park where these plants grew received little or no artificial watering, perhaps accounting for the eventual death of most of the plants, after which the mature wood sample was taken. Although one tends to assume that localities under cultivation have greater moisture availability than those in the wild, this may not in fact be true. The wood sample studied of *C. trimerum* (*Oxford 10768*) was taken from the wild, and is probably a portion of the same collection studied by Heimsch (1942), who did not, however, cite the specimens he used. I am grateful to Dr. Jeff Burley of the Oxford Forestry Institute for loan of a wood-section slide of *C. trimerum*.

Wood samples were available in dried condition. Portions were boiled, stored in aqueous 50% ethyl alcohol, and sectioned on a sliding microtome. Wood of *C. pulverulentum* contains exceptionally thick-walled fibers, and one collection (*Bramwell s.n.*) was soaked in ethylene diamine prior to sectioning; this resulted in improvement of sectioning. Sections were stained with safranin and lightly counterstained with fast green. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Means are based on the average of 25 measurements, except for vessel wall thickness, libriform fiber wall thickness, and diameter of libriform fiber at widest point; for these three features, a few typical conditions were selected for measurement. Vessel diameter includes the thickness of the wall. The figure for vessels per group was obtained on the basis that a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. The figure for vessels per mm² counts all pores rather than counting a group of pores as one.

ANATOMICAL DESCRIPTIONS

CNEORUM PULVERULENTUM (*Bramwell s.n.*) (Fig. 1-5).—Growth rings weakly present; latewood vessels slightly narrower (Fig. 1). In some years a thin band of terminal axial parenchyma (often only a single cell layer thick) is present. Vessels often in radial multiples (Fig. 1). Mean number of vessels per group, 1.89. Mean number of vessels per mm², 234. Mean vessel diameter, 24 μ m. Mean vessel element length, 288 μ m. Mean vessel wall thickness, 3.0 μ m. Perforation plates simple. Lateral wall pitting of alternate circular bordered pits averaging 3.2 μ m in diameter on vessel-vessel contacts; vessel-axial parenchyma pits sparser, about 4.0 μ m in diameter. Grooves interconnecting apertures of pits adjacent in a helix

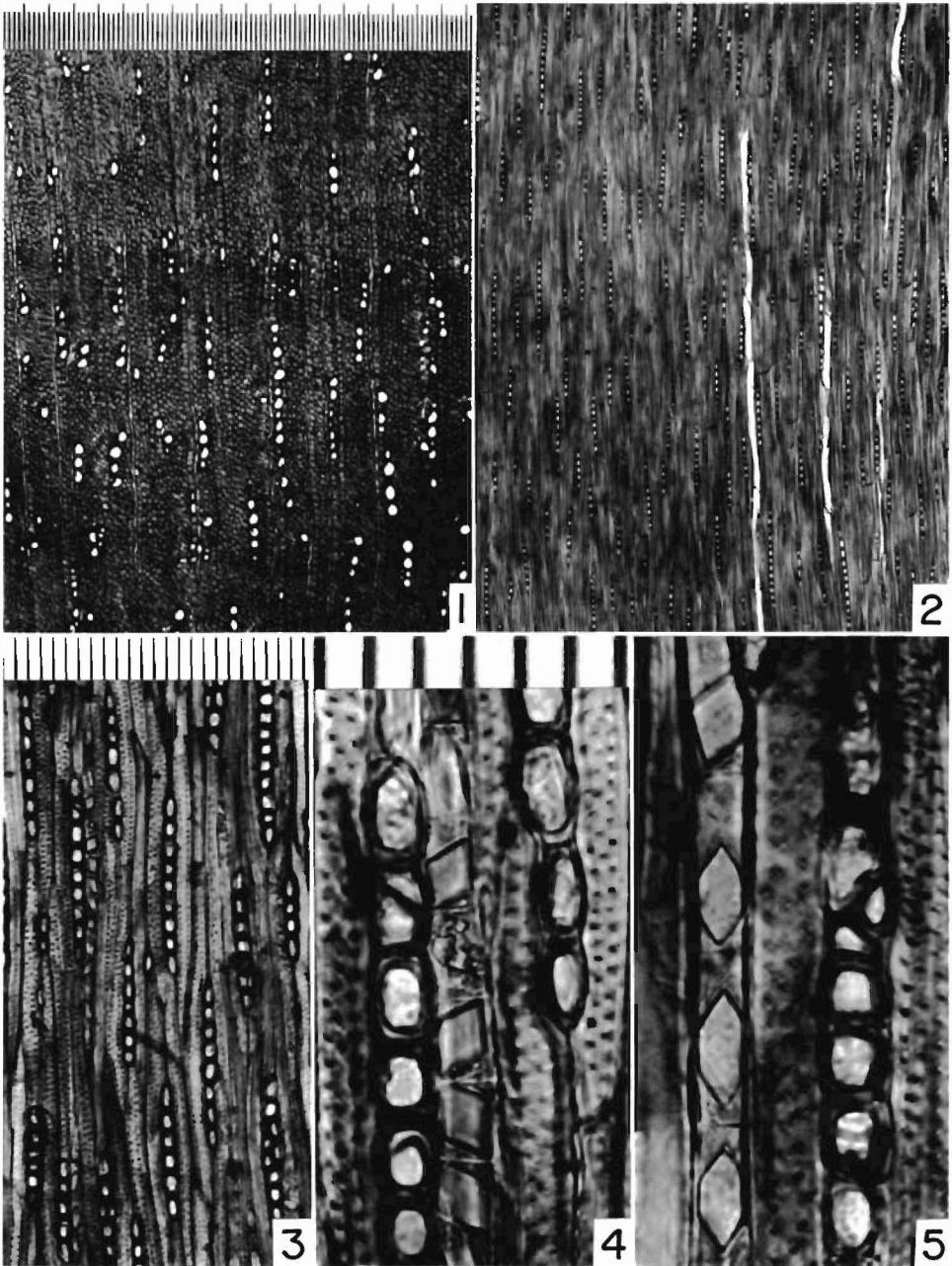


Fig. 1–5. Wood sections of *Cneorum pulverulentum* (D. Bramwell s.n.).—1. Transection; vessels in radial multiples; fibers thick walled.—2. Tangential section; rays almost exclusively uniseriate.—3. Portion of tangential section to show thick-walled ray cells, strand of crystalliferous parenchyma.—4. Portion of tangential section to show thick-walled ray cells, strand of thin-walled crystalliferous parenchyma.—5. Portion of tangential section, elongate nature of parenchyma cells and hexagonal nature of crystals evident. (Fig. 1–2, magnification scale above Fig. 1 [finest divisions = 10 μ m]; Fig. 3, scale above Fig. 3 [divisions = 10 μ m]; Fig. 4–5, scale above Fig. 4 [divisions = 10 μ m].)

present in walls of at least some latewood vessels. Imperforate tracheary elements are mostly libriform fibers with minute simple pits; some vasicentric tracheids also present (Fig. 3). Mean libriform fiber diameter at widest point, 14 μm . Mean libriform fiber length, 618 μm . Mean libriform fiber wall thickness, 4.0 μm . A few vasicentric parenchyma strands are adjacent to vessels or vessel groups (strand = 2 cells in length). Terminal parenchyma bands one (rarely more) cell in thickness present at ends of some growth rings. Parenchyma cells also present in diffuse arrangement, but all diffuse parenchyma consists of crystalliferous strands in which each cell is thin walled and contains a single large crystal (Fig. 4, 5), sometimes with additional small crystals. Uniseriate rays much more common than biseriate rays, no triseriate rays observed (Fig. 2, 3). Ray cells all procumbent except for cells at tips of rays, which vary from procumbent to square (Fig. 4, 5). Ray cell walls about 1.5 μm in thickness (Fig. 4, 5). Mean biseriate ray height, 130 μm . Mean uniseriate ray height, 112 μm . Wood nonstoried. No amorphous deposits in wood observed.

CNEORUM PULVERULENTUM (Carlquist 2482).—Qualitative features as above. Quantitative features as follows. Mean number of vessels per group, 2.12. Mean number of vessels per mm^2 , 231. Mean vessel diameter, 31 μm . Mean vessel element length, 266 μm . Mean vessel wall thickness, 3.4 μm . Vessel-vessel pits about 3 μm in diameter, vessel-parenchyma pits about 4 μm in diameter. Mean libriform fiber diameter at widest point, 14 μm . Mean libriform fiber length, 549 μm . Mean libriform fiber wall thickness, 5.0 μm . Mean height of biseriate rays, 127 μm . Mean height of uniseriate rays, 118 μm .

CNEORUM PULVERULENTUM (Carlquist 2530).—Qualitative features as in *Bramwell s.n.*; quantitative features as follows. Mean number of vessels per group, 1.96. Mean number of vessels per mm^2 , 245. Mean vessel diameter, 30 μm . Mean vessel element length, 223 μm . Mean vessel wall thickness, 14 μm . Vessel-vessel pits about 2.8 μm in diameter, vessel-axial parenchyma pits about 3.8 μm in diameter. Mean libriform fiber diameter at widest point, 14 μm . Mean libriform fiber length, 477 μm . Mean libriform fiber wall thickness, 4.8 μm . Mean height uniseriate rays, 117 μm (biseriate rays very few).

CNEORUM TRICOCCON (Carlquist 20-VI-1971) (Fig. 6–10).—Growth rings present, vessels markedly wider in earlywood (Fig. 6). Vessels often grouped into diagonal aggregations (Fig. 6). Mean number of vessels per group, 6.0. Mean number of vessels per mm^2 , 591. Mean vessel diameter, 19 μm . Mean vessel element length, 288 μm . Mean vessel wall thickness, 2.4 μm . Perforation plates simple. Vessel-vessel pits about 3 μm in diameter. Helical thickenings present in all vessels as well as in vasicentric tracheids (Fig. 8). Imperforate tracheary elements are libriform fibers with minute simple pits; numerous vasicentric tracheids are also present within the diagonal vessel groups, where the vasicentric tracheids resemble the narrowest vessel elements in diameter. Mean libriform fiber diameter, 14 μm . Mean libriform fiber length, 660 μm . Mean libriform fiber wall thickness, 2.8 μm . Axial parenchyma cells 1–2 near some vessels, thus vasicentric scanty; these parenchyma cells in strands of two. Terminal parenchyma present (usually a single layer of cells) at the ends of some of the growth rings. A very small number of crystalliferous axial parenchyma strands with a diffuse distribution also present (Fig. 10). Multiseriate (biseriate plus triseriate) rays about as frequent as uniseriate

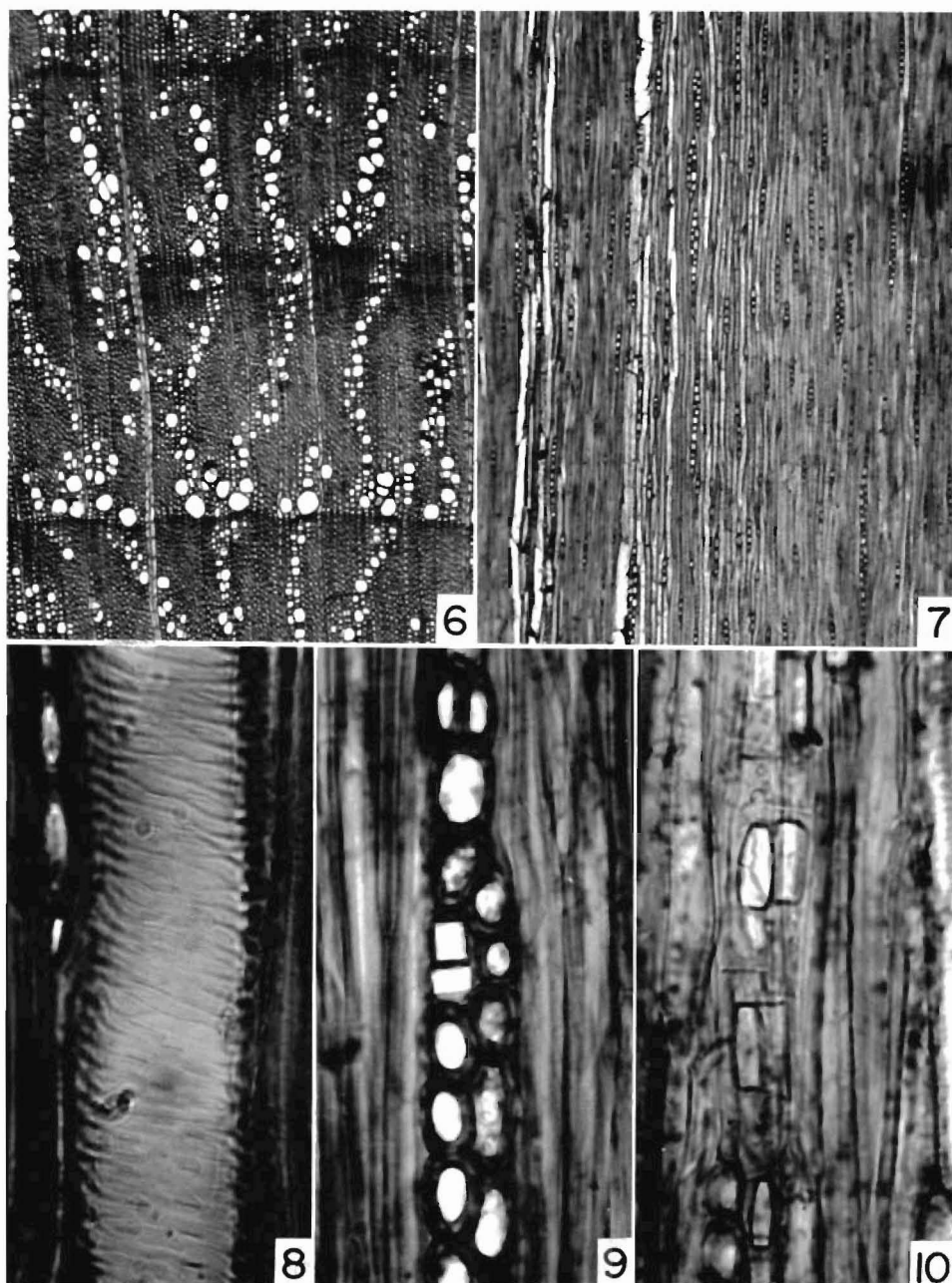


Fig. 6–10. Wood sections of *Cneorum tricoccon* (Carlquist 20-VI-1971).—6. Transection; diagonal aggregations of vessels, growth rings present.—7. Tangential section; uniseriate and biseriate rays about equally abundant.—8. Vessel wall from tangential section; helical thickenings present.—9. Biseriate ray from tangential section; two crystals in ray cell, center.—10. Crystals in thin-walled elongate chambered diffuse parenchyma cells, from tangential section. (Fig. 6–7, magnification scale above Fig. 1; Fig. 8–10, scale above Fig. 4.)

rays (Fig. 7). Triseriate rays less frequent than biseriate rays. Most ray cells procumbent (Fig. 9), a few erect or square cells scattered throughout rays. Rhomboidal crystals (one per cell) present in some ray cells (Fig. 9). Bordered pits present on some ray cell walls, pits otherwise simple. Ray cells 1–1.5 μm thick (Fig. 9). Mean multiseriate ray height, 232 μm . Mean multiseriate ray width, 2.36 cells. Mean height uniseriate rays, 82 μm . Wood nonstoried. Tannin deposits in some cells.

CNEORUM TRIMERUM (Oxford 10768) (Fig. 11–16).—Growth rings absent or faint, possibly demarcated by occasional bands of terminal parenchyma (Fig. 11, center). Vessels in small cluster or short radial multiples (Fig. 11). Mean number of vessels per group, 2.16. Mean number of vessels per mm^2 , 42. Mean vessel diameter, 55 μm . Mean vessel element length, 157 μm . Mean vessel wall thickness, 2.5 μm . Perforation plates simple. Vessel-vessel pits alternate, about 2.5 μm in diameter (Fig. 14). Vessel-axial parenchyma pits about the same or laterally elongate. Helical grooves interconnect pit apertures in many vessels (Fig. 14). A pair of inconspicuous thickening bands flanking the grooves may be seen in a few vessels. All imperforate tracheary elements are libriform fibers with minute simple pits. No vasicentric tracheids observed. Mean libriform fiber diameter at widest point, 16 μm . Mean libriform fiber length, 265 μm . Mean libriform fiber wall thickness, 2.5 μm . Axial parenchyma aliform or aliform-confluent (Fig. 11, see also right half of Fig. 12). Terminal parenchyma also present (Fig. 11, center). Axial parenchyma cells mostly not subdivided into strands (Fig. 12), a few cells in strands of two (Fig. 15). No diffuse parenchyma present. Multiseriate rays more common than uniseriate rays (Fig. 12). Rays composed of procumbent cells (Fig. 13), some cells approaching a square shape. Walls of ray cells thin but lignified (Fig. 16), about 0.5 μm thick. Height of multiseriate rays, 128 μm . Mean width of multiseriate rays, 2.2 cells. Mean height of uniseriate rays, 63 μm . Small crystal-like structures seen in a very small number of ray and axial parenchyma cells (Fig. 16), but these may be artifacts rather than calcium oxalate crystals. Storying clearly present in vessels, axial parenchyma, and a few wider libriform fibers adjacent to axial parenchyma (Fig. 12). Amorphous deposits not observed.

ECOLOGICAL CONCLUSIONS

The woods of the specimens from cultivation seem to be altered little or not at all compared to the quantitative features observed in the wild specimens, and the comparisons undertaken here assume the woods studied are typical for the respective species. The Mediterranean coasts where *C. tricocon* is native have warm, dry summers and cool, moderately wet winters with occasional frosts. At least with respect to temperatures, the Canary Island localities where *C. pulverulentum* occurs are more moderate, because these insular lowlands are frost-free. However, the Canarian localities probably receive no more rainfall than the *C. tricocon* localities (comparisons cannot be made because recording stations on the Canary Islands are not close to the *C. pulverulentum* localities). *Cneorum trimerum* occurs in exposed sites in montane eastern Cuba where the rainfall, humidity, and therefore water availability are greater than for either of the two other species. Frost is probably absent in the *C. trimerum* localities. Thus, in terms of increasing water availability, the three species form a series: *C. tricocon*, *C. pulverulentum*, *C. trimerum*.

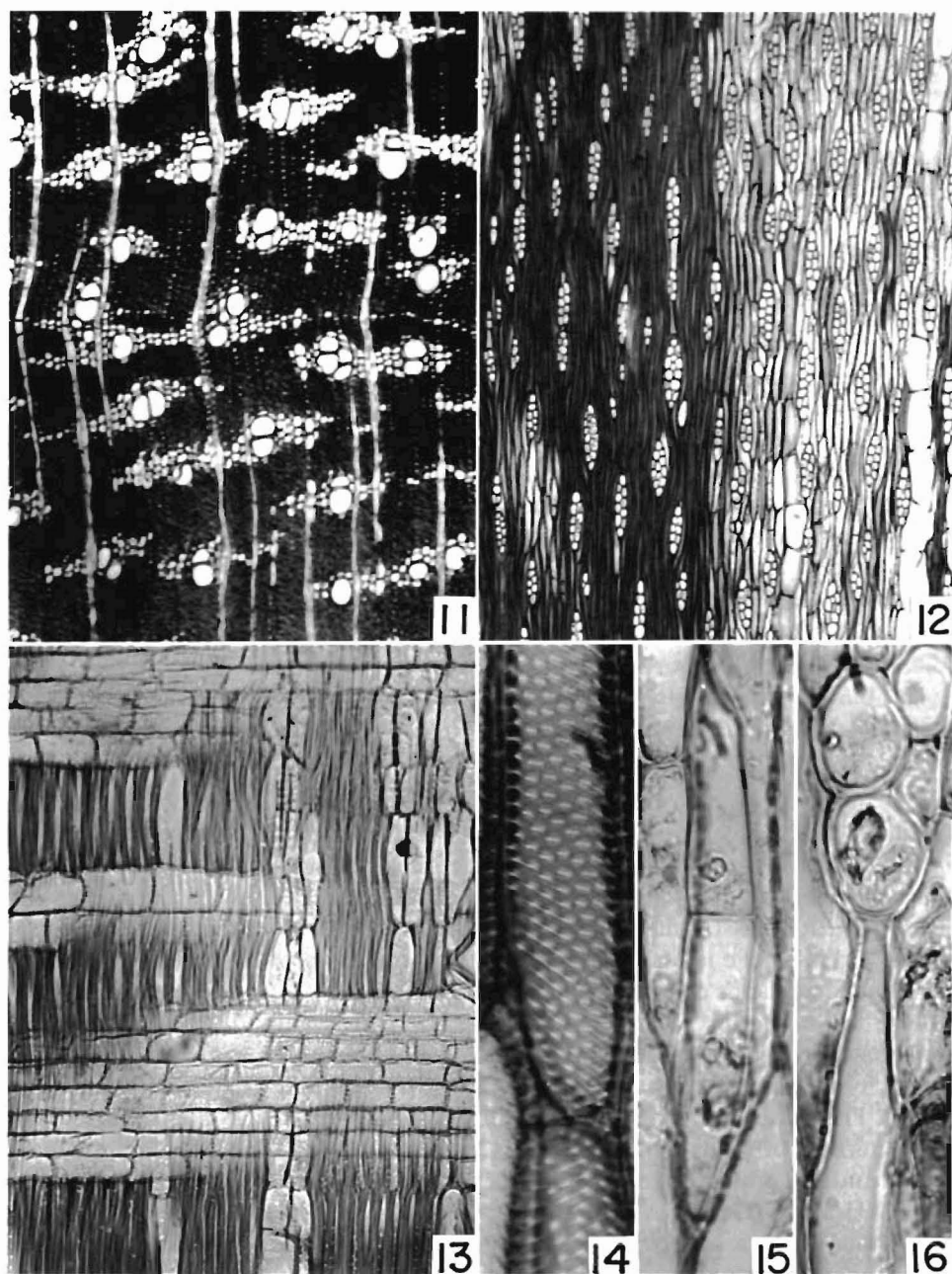


Fig. 11–16. Wood sections of *Cneorum trimerum* (Oxford 10768).—11. Transection; aliform and aliform-confluent parenchyma adjacent to vessels; a terminal band of parenchyma, center.—12. Tangential section; storied axial parenchyma and vessels occupy right portion of photograph.—13. Radial section; all ray cells are procumbent.—14. Vessel wall from tangential section; grooves interconnect pit apertures (center).—15. Two-cell strand of axial parenchyma from tangential section; one small crystal-like object is present in each of the two cells.—16. Portion of ray (above) and axial parenchyma strand (right), showing thin walls; small crystal-like objects present. (Fig. 11, 12, scale above Fig. 1; Fig. 13, scale above Fig. 3; Fig. 14–16, scale above Fig. 4.)

The Mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm²; Carlquist 1977) continues to prove a reliable indicator because the three features are independent adaptations to safety in wood. For the species in this study, the Mesomorphy values are as follows: *C. pulverulentum* (collections averaged), 29; *C. tricocon*, 9; *C. trimerum*, 207. The sequence of values parallels the climatic severity of the localities as described above. The large gap between *C. trimerum* and the other two species probably shows not so much the effect of frost, but of prolonged summer drought. The number of vessels per group is most elevated in the species from the most xeric localities, *C. tricocon*.

Another wood feature that parallels the above series is presence of vasicentric tracheids. *Cneorum trimerum* lacks vasicentric tracheids; they are relatively few in *C. pulverulentum* (mostly, but not exclusively, in latewood); they are abundant in *C. tricocon*. Presence of vasicentric tracheids was reported earlier in *C. tricocon* (Carlquist 1985). Vasicentric tracheid presence is characteristic of shrubs in Mediterranean-type climates; presence and relative abundance of vasicentric tracheids are indicators of degree of xeromorphy (Carlquist 1985). The prominent diagonal groupings of vessels in *C. tricocon* is related to abundance of vasicentric tracheids as well as to xeromorphy: diagonal vessel aggregations occur only in species that have vasicentric tracheids (or, in a few cases, very narrow vessels) and are also in relatively xeric areas (Carlquist 1987).

RELATIONSHIPS OF CNEORACEAE

Heimsch (1942), on the basis of wood studies, claimed that Cneoraceae are nearer to Rutaceae than to Zygophyllaceae. The current systems most widely cited (Thorne 1976; Dahlgren 1980; Takhtajan 1980; Cronquist 1981) place Cneoraceae in an order usually termed Rurales (sometimes Sapindales) near Rutaceae and Simarubaceae. At least some members of both of these families share the following features with at least some species of Cneoraceae: vessels with simple perforation plates and alternate lateral wall pitting; libriform fibers with simple pits present; vasicentric tracheids present; axial parenchyma aliform-confluent or terminal plus diffuse crystalliferous strand parenchyma; rays predominantly (or exclusively) uniseriate, with cells procumbent or mostly so; crystals in some ray cells; axial parenchyma and vessels storied (data from Metcalfe and Chalk 1950; Carlquist 1985). The diffusely distributed crystalliferous strand parenchyma is particularly characteristic of many genera of Rutaceae (Heimsch 1942; Metcalfe and Chalk 1950). Indeed, one could match almost exactly the wood of *Cneoridium dumosum* (Nutt.) Hook. f. (Carlquist 1985, p. 48) with that of *Cneorum tricocon*, although that should be construed more as a parallelism due to evolution of a rutalean plant in similar ecological conditions than to close genetic relationship between the two species.

Cneoridium is the only genus of Rutaceae reported to have "resin cells" in leaves (Metcalfe and Chalk 1950), although in both Cneoraceae and Simarubaceae, secretory cells presumably corresponding to that term are common in leaves (Metcalfe and Chalk 1950). The secretory cavities so common in Rutaceae do not occur in Cneoraceae, and the use of the term "oil gland" (Doggett in Heywood 1978) in Cneoraceae is a misnomer.

Pollen morphology does not clearly ally particular families with Cneoraceae,

Table 1. Wood characteristics of the species of *Cneorum*.

<i>C. pulverulentum</i>	<i>C. tricocon</i>	<i>C. trimerum</i>
Vessels grouped radially	Vessels in diagonal aggregations	Vessels in short radial chains or in clusters
Vessel walls grooved in late-wood	Vessels with helical thickenings	Vessel walls grooved in part
Fibers very thick walled	Fibers thick walled	Fibers thin walled
Vasicentric tracheids not abundant	Vasicentric tracheids abundant	Vasicentric tracheids absent
Axial parenchyma vasicentric scanty, terminal, diffuse crystalliferous	Axial parenchyma vasicentric scanty, terminal, diffuse crystalliferous	Axial parenchyma aliform-confluent, terminal
Rays mostly uniseriate	Rays biseriate and uniseriate equally	Rays mostly biseriate
No crystals in ray cells	Crystals in ray cells	Crystals absent in rays?
Wood nonstoried	Wood nonstoried	Vessels and axial parenchyma storied

but relationship with Rutaceae or Simarubaceae is not ruled out on the basis of Erdtman's (1953) data.

Families not within Rutales but peripheral to that order show a somewhat lesser degree of resemblance to features of Cneoraceae. For example, in the Oxalidaceae, a family usually placed in the same superorder as Rutales (e.g., Rutiflorae) but in Geraniales, *Averrhoa* has scanty vasicentric parenchyma plus diffuse crystalliferous chambered parenchyma, a distinctive combination seen in Cneoraceae and other rutalean families.

Many of the features mentioned above may also be found in Euphorbiaceae, a family not generally considered close to Rutales. Euphorbiaceae is considered because it has been mentioned in connection with Cneoraceae: *Cneorum trimerum* was originally described as a genus in Euphorbiaceae under the name *Cubincola trimera* Urb. The resemblances in wood anatomy between Cneoraceae and Euphorbiaceae are very likely attributable more to the heterogeneity of Euphorbiaceae than to close relationship with Cneoraceae: when one lists the features of a large family highly diverse with respect to wood anatomy, one is likely to find more characters like those of a particular family than if one compares two similarly distant families both of which are relatively uniform with respect to wood anatomy. The diffuse-in-aggregates type of axial parenchyma characteristic of most Euphorbiaceae does not occur in Cneoraceae.

The preponderance of evidence does seem to place Cneoraceae within Rutales. The family does not appear to be closer to one particular family, however. Although Rutaceae and Simarubaceae have been prominently mentioned above, nearly as many resemblances between Cneoraceae and Anacardiaceae or Sapindaceae may be found.

GENERIC CONSTITUTION OF CNEORACEAE

The three species of the family have been treated as one genus by some authors, but Tieghem (1899) segregated *C. pulverulentum* on the basis of its tetramerous flowers, and Erdtman (1953) added a pollen difference (renaming Tieghem's genus

for nomenclatural reasons). The Cuban species *C. trimerum* was originally named as *Cubincola*, but this genus was described in Euphorbiaceae, and segregation from *Cneorum* was therefore not intended. When one compares the wood anatomy of the three species in Table 1, a notable picture emerges.

Several conclusions may be reached from this comparison. The differences among the species are more numerous than is typical within most genera. The geographical disjunction of the three species is unusual, however, and the differences in wood anatomy may be related to those disjunctions. A few of the differences in Table 1 are related to ecology, as noted in the Ecological Conclusions (e.g., abundance of vasicentric tracheids), but most features in Table 1 do not bear a direct relation to ecology (e.g., crystal distribution, presence of storying).

The species most distinctive on the basis of its tetramerous corolla and hexacolpate pollen is *C. pulverulentum*. Wood of *C. pulverulentum* is more similar to wood of *C. tricocon* than to that of *C. trimerum*. Thus if wood anatomy were used as a criterion, *C. trimerum* would be the species most worthy of generic segregation. That treatment would likely not be accepted because features of gross morphology do not differentiate *C. trimerum* markedly from *C. tricocon*.

Considering evidence currently available from wood anatomy as well as from other sources, the most advisable treatment would seem to be recognition of a single genus. Construction of three subgenera is a possible treatment, but definition of these offers much the same problems as does recognition of three genera.

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